THE GENERAL FEEDING ECOLOGY OF POSTLARVAL FISHES IN THE NEWPORT RIVER ESTUARY[1]

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ABSTRACT

Food preferences, feeding intensity and chronology, evacuation rates, and daily rations were determined for postlarval stages of Atlantic menhaden, *Brevoortia tyrannus* (25-32 mm); pinfish, *Lagodon rhomboides* (16-20 mm); and spot, *Leiostomus xanthurus* (17-24 mm). Four copepod taxa, *Centropages*, *Temora*, *Acartia*, and Harpacticoida, made up 76-99% of the total gut contents. Postlarval feeding intensity was greatest during early daylight hours. Postlarval menhaden lost an estimated 60% of their orginal gut contents due to the stress of handling and capture. Similar stress caused no food loss in either postlarval pinfish or spot. Gastrointestinal evacuation of copepods and *Artemia* nauplii were described by linear regression. Evacuation rates varied directly with the amount of food in the gut. Rate constants were used in conjunction with information on the chronology of gut contents to determine daily rations. Daily ration estimates as a percent of the fish's wet body weight were: menhaden, 4.9%; pinfish, 3.5%; spot, 4.3% and 9.0%. The ration estimates for spot in terms of calories per fish per day were similar to the metabolic needs estimated from oxygen consumption measurements but were lower than the estimates from oxygen consumption for menhaden and pinfish.

Larval and postlarval fish are significant consumers in aquatic ecosystems, yet our knowledge of their feeding habits and daily food consumption is incomplete. This paper deals with the general feeding ecology of the postlarval stages of three common estuarine fishes. Four major aspects are discussed. These include 1) food preferences, 2) feeding intensity and chronology, 3) evacuation rate, and 4) daily ration.

Postlarval Atlantic menhaden, *Brevoortia tyrannus*; pinfish, *Lagodon rhomboides*; and spot, *Leiostomus xanthurus*, were collected during March of 1972 and 1973 from the Newport River estuary, Carteret County, N.C. The fish (hereafter referred to as larvae) were taken near Pivers Island, approximately 2.5 km inside the Beaufort Inlet. Pinfish and spot were collected using a seine and dip nets, while menhaden were captured in a channel net (Lewis et al. 1970) and with dip nets. One additional group of samples was collected in bongo nets. Most fish were frozen immediately following capture, thus stopping their digestive processes. The only exceptions to preservations by freezing were the bongo net samples which were placed in 5% Formalin.[3]

Food preferences were determined by examining the contents of entire digestive tracts. The gut contents from 120 fish of each species collected throughout the day were combined and individual food items identified, counted, and measured. Copepodite and adult copepods composed 99-100% (by both number and volume) of the identifiable food items in the digestive tracts. The average-sized copepod fed upon by each larval species was determined by measuring 100 copepods chosen from the combined digestive tract contents of all larvae collected in a 24-h period.

Diel periodicity of digestive tract contents indicated the intensity and chronology of feeding by the larvae. Twenty fish of each species were collected at 4-h intervals for 24 consecutive hours.

Larval evacuation rates for copepods and for *Artemia salina* were determined from laboratory experiments performed at 15°-17°C and 25-30‰; conditions which typify larval collection sites during March. Copepod evacuation was determined by collecting larvae from the estuary, placing them in food-free seawater tanks, and observing the decrease in their gut contents through time. At the time of initial capture

[1]This research was supported through a cooperative agreement between the National Marine Fisheries Service and the U.S. Atomic Energy Commission.

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[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Manuscript accepted March 1974.
FISHERY BULLETIN: VOL. 73, NO. 1, 1975.

and every 3 or 4 h thereafter, at least 10 fish were killed and the copepods present were counted. Evacuation of newly hatched *Artemia* nauplii was measured by allowing unfed larvae to feed to satiation on high prey densities (0.3 to 3.0 nauplii/cm^3), placing them in a food-free environment, and then periodically removing larvae for determination of remaining gut contents. Sampling of both copepod- and *Artemia*-fed fish continued periodically from the time of feeding until more than one-half of the fish had empty tracts.

Linear regression equations of log-transformed data were used to describe the evacuation process (Peters et al. 1974). The equations were of the form:

$$\log_{10} C = A + Bt$$

where C = 1 + the mean number of copepods or *Artemia* present in the gut
t = time
$A + B$ = regression terms

Instantaneous evacuation rates were calculated from the equation $\frac{dC}{dt} = 2.303\ BC$ (Peters and Kjelson in press).

Daily rations were calculated using information on diel periodicity of gut content and instantaneous evacuation rates. Previous calculations of fish rations (Bajkov 1935; Seaburg and Moyle 1964) have assumed a constant evacuation rate, but more recent data (Tyler 1970; Elliot 1972) indicate that digestive rate changes with the quantity of food in the digestive tract.

Our method of calculating daily ration (Peters and Kjelson in press) accounts for changes in evacuation rate which accompany diel changes of feeding intensity. To calculate the rations, we first determined an average instantaneous evacuation rate (in copepods per hour) for each of the 4-h sampling periods in the diel cycle. This average rate was the geometric mean of the instantaneous evacuation rates at the beginning and end of the period. Since each period lasted 4 h, the estimate of food evacuated during the period was four times the average instantaneous hourly evacuation rate. The total food evacuated per day was achieved by summing the six 4-h evacuation estimates, and is an estimate of the daily ration, because average ingestion rate must equal the rate at which material leaves the gut whether by assimilation or expulsion.

Daily rations were calculated initially as copepods per fish per day and then transformed to percent of the larval body weight and calories per fish per day. Dry weights of ingested copepods were estimated from the length-weight relationship:

$$W = 6.274L - 0.153$$

where W = dry weight in micrograms
L = copepod length, based on Heinle's (1966) data for all stages of *Acartia tonsa*

Copepod dry weights were converted to wet weights using a factor of 9.1 based upon our measurements of the wet/dry ratio for zooplankton, and were compared to wet weights of the fish to compute the daily ration as a percent of live body weight. Daily caloric intake was computed using our estimation of 0.555 cal/mg wet weight of an average size copepod during March, based on microbomb calorimeter measurements of mixed estuarine zooplankton (Thayer et al. 1974).

FOOD PREFERENCES

The larvae we collected were feeding primarily upon copepods, a common food source for both freshwater and marine fish larvae (Werner 1969; May 1970). Copepods composed 99% (by volume and number) of the gut contents of larval spot, pinfish, and menhaden (Table 1). Four copepod taxa (*Centropages*, *Temora*, *Acartia*, and Harpacticoida) were dominant. Diatoms, amphipods, barnacle larvae, crab zoea, and ostracods, although present in some larvae, were rare.

TABLE 1.—Relative (percent) composition by number of the major taxa in the total gut contents of three species of larval fish.

Taxa	Larval species		
	Pinfish	Spot	Menhaden
Harpacticoida	32	32	22
Centropages	28	28	40
Temora	3	21	6
Acartia	13	8	30
Other copepods	23	10	1
Other organisms	1	1	1
Total	100	100	100

Prey size is an important factor in determining the individuals selected by planktivorous fish (Ivlev 1961; Brooks and Dodson 1965; Kjelson 1971). The larval fish we studied appeared to restrict the majority of their feeding to items of a size ranging between 300 and 1,200 μm. Our observations of the mean length of ingested copepods showed that the larger menhaden larvae (26-31 mm, $\bar{x}$ = 29 mm TL) ingested 750-μm copepods with an estimated copepod wet weight of 0.04 mg, while the smaller spot (17-22 mm, $\bar{x}$ = 19 mm TL) and pinfish larvae (16-20 mm, $\bar{x}$ = 18 mm TL) fed upon 600-μm copepods with an estimated wet weight of 0.03 mg. Small zooplankters such as copepod nauplii, barnacle larvae, or small adult copepods such as *Oithona* (all present in the plankton tows) were rarely found in gut contents. Copepods larger than 1.2 mm were in the plankton, but were rarely consumed. Perhaps copepods were the only food items of the appropriate size present in sufficient abundance. Had we collected smaller larvae, it is possible food preferences may have been for smaller food items such as copepod nauplii and copepodites and adults of small-sized species as well as phytoplankton. May (1970) stressed the fact that larval fish require progressively larger prey as they grow. However, since larvae smaller than the size we collected are rarely found in the Newport River estuary, we feel our data indicates that smaller planktonic forms are relatively unimportant to the larval fish studied in this estuary.

Thayer et al. (1974) found that as a yearly average, copepods represented 81% of the zooplankton numbers and 85% of the zooplankton biomass retained by a No. 10 mesh plankton net. Since larval fishes enter the Newport River estuary during winter and spring, the consumption of copepods by these three larval species may, in part, explain the decrease in copepod abundance observed by Thayer et al. (1974) during this period. They noted that the four copepod taxa utilized by these larvae decreased from a mean of 81% of the copepod biomass during March 1970 and 1971 to a mean of 48% of the biomass during the summer.

FEEDING CHRONOLOGY AND INTENSITY

All three larval fishes had the highest food content in their digestive tracts during daylight hours (Figures 1-3). Periodicity of gastrointestinal contents indicates that each population begins feeding near dawn and reaches a maximum gut fullness near midday. The rapid single increase in the gut content of the three species indicates they have one major burst of feeding activity per day (Figures 1-3). Other studies (Blaxter 1965; Schumann 1965; Braum 1967; June and Carlson 1971) have shown that larval fish generally do not have food within their digestive tracts when captured at night, suggesting that larval fish do not feed at low light intensities.

Considerable variation was observed in the amounts of food present in larval guts (Figures 1-3). The variation is probably due to differences in prey abundance or capture and handling techniques, although other factors such as fish size and copepod size may also be important. During our 24 h sampling the variation in numbers of copepods in individual fish was high at some times and low at others. The ratio of the standard error of the estimate to the mean varied from 4 to 48% for spot with a mean of 21%; for menhaden the ratio varied from 0 to 100% with a mean of 40%; and for pinfish it varied from 0 to 100% with a mean of 43%. Spot larvae

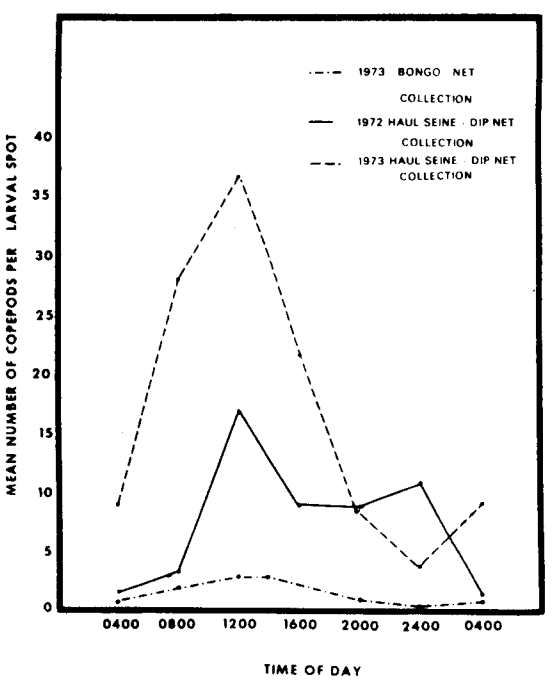

FIGURE 1.—Variation in diel cycle of gastrointestinal contents in postlarval spot.

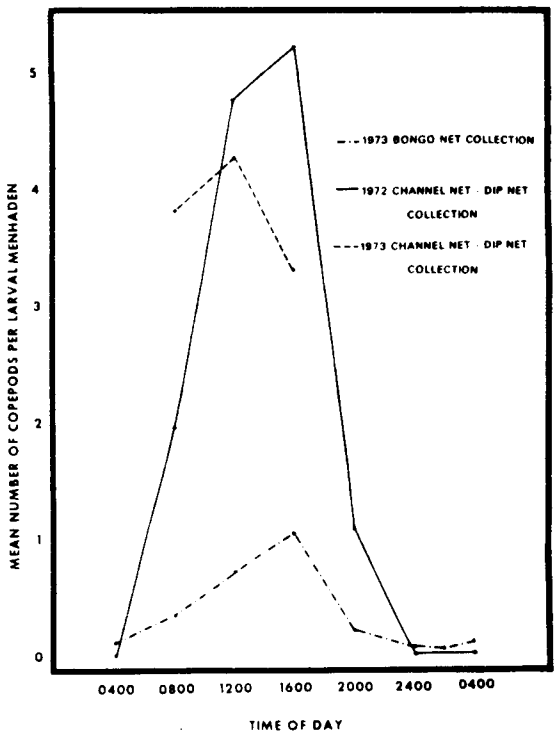

FIGURE 2.—Variation in diel cycle of gastrointestinal contents in postlarval Atlantic menhaden.

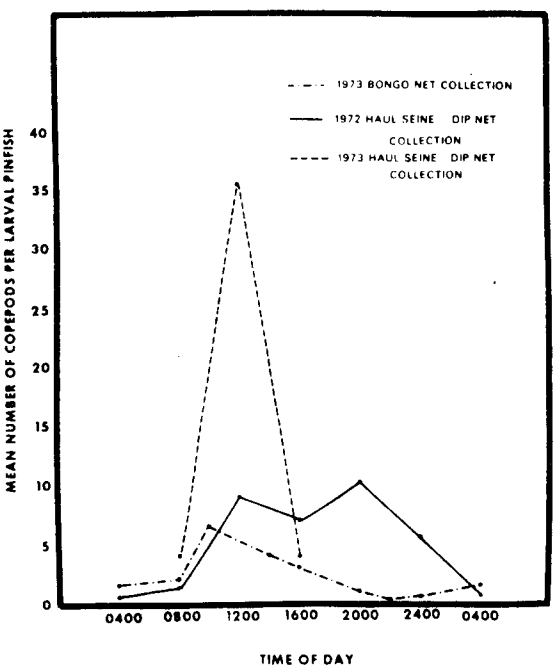

FIGURE 3.—Variation in diel cycle of gastrointestinal contents in postlarval pinfish.

(18-24 mm, $\bar{x}$ = 21.5 mm) collected by dip net at one location and between 0830 and 1030 h over a 4-day period had little variation in their mean gut contents. Spot larvae collected 2 April averaged 25.3 copepods/fish (SE = 2.3), on 3 April, 21.3 (SE = 2.0), and on 5 April, 26.3 (SE = 3.7). The similarity of food quantity in the larval digestive tracts suggests that prey abundance may have remained relatively constant over the 4-day period thus allowing the fish to consume similar amounts of food.

ESTIMATES OF LARVAL GUT CAPACITIES

Laboratory feeding experiments were conducted at 15°-16°C to estimate the maximum gut capacity of the larvae. The fish were fed high densities of *Artemia* nauplii until their digestive tracts were completely packed from esophagus to anus. Menhaden (28-32 mm, $\bar{x}$ = 30 mm TL) fed for 20 min on a concentration of *Artemia* nauplii, 3 nauplii/cm^3, had an average of 145 nauplii/fish in their digestive tracts (SE = 9.6). Spot larvae (19-23 mm, $\bar{x}$ = 21 mm TL) fed for 15 min on 0.3 nauplius/cm^3 had an average of 89 (SE = 7.0) nauplii/fish; and pinfish (16-20 mm, $\bar{x}$ = 18 mm TL) fed for 1 h on 0.3 nauplius/cm^3, had an average of 75 (SE = 15.1) nauplii/fish. By comparing individual *Artemia* and copepods of the four major taxa side by side under a microscope, we estimated that the volume of two 450-μm *Artemia* nauplii were equivalent to that of one 650-μm copepod. Using 0.5 as a conversion factor, we calculated maximum gut capacities in terms of copepods. Menhaden larvae of 30 mm have a gut capacity of 72 copepods, 21-mm spot a gut capacity of 44 copepods, and 18-mm pinfish a gut capacity of 37 copepods. These estimates of gut capacity were comparable to the maximum numbers of copepods observed in the digestive tracts of larval fish collected in the estuary for spot (36.5 copepods/fish) (Figure 1) and pinfish (35.3 copepods/fish) (Figure 3), but not for menhaden (5.2 copepods/fish) (Figure 2). This large difference between gut capacity and observed gut contents suggests that menhaden larvae either feed very little under natural conditions, and never approach the estimated maximum gut capacity or capture and/or handling causes them to regurgitate or defecate causing inaccuracy in our estimate of natural gut content. To test

the latter possibility, we performed a variety of experiments to determine if handling and capture technique influences the quantities of food observed in the larval gut.

EFFECTS OF SAMPLING TECHNIQUE ON GUT CONTENT

Larvae of all three species were first collected by a 3-m channel net with an attached live box. Captured fish were counted, identified, divided into two groups, and transferred (underwater) into separate containers. One group of fish was anesthetized with 0.12 g/liter MS-222 (tricaine methanesulfonate) and then dissected, while the other group was transferred carefully into the posterior end of a 20-cm bongo net (keeping them underwater throughout transfer). The net was towed for 5 min, and after retrieval the larvae were removed, identified, and counted to assure that none were lost and that no new larvae were captured. The fish were then dissected to determine the number of copepods present in their guts. Menhaden lost 68% of their gut contents when exposed to the stress of bongo tows, whereas gut contents of larval spot and pinfish before and after the bongo tow did not differ statistically (Table 2). The amounts of food present in all three species of larvae collected at the Beaufort Inlet in the 24-h bongo samples were lower than the food quantities observed in larvae collected by the other techniques inside the estuary (Figures 1-3). Thus, factors other than the stress of capture may be responsible for the low gut contents in larvae collected in the bongo nets: 1) copepod abundance may have been lower at the Beaufort Inlet sampling site than further inside the estuary, 2) the use of Formalin (restricted to bongo samples) to kill and preserve the larvae may have caused defecation of the copepods prior to analysis (June and Carlson (1971) showed that larval menhaden when placed in Formalin had violent spasms accompanied by defecation), and 3) larvae collected in midchannel by bongo nets may not be feeding as actively since they are exposed to a greater tidal current (perhaps the protected inshore waters of the estuary may allow the larvae to feed more efficiently and result in fish with greater numbers of prey in their digestive tracts).

No significant differences were observed in the food contents of spot larvae collected by routine seining and those collected by seining with a more gentle sampling technique (Table 3). In routine seining, the larvae were picked out of the seine as it lay on the shore and placed in a bucket of ice water. The gentle sampling technique consisted of surrounding a body of water with the seine and then concentrating the larvae, taking care that fish were not forced against the net. Once concentrated, the larvae were dipped out of the water in a bucket and anesthetized with MS-222. The results of our sampling experiments indicate that routine field sampling techniques used to collect spot and pinfish larvae probably caused little loss of food from the digestive tracts.

TABLE 2.—The effect of bongo net tow stress upon the amount of food observed in larval menhaden, pinfish, and spot.

Capture technique	Menhaden[1]	Pinfish[2]	Spot[3]
	Mean number copepods/fish ± one SE		
Channel net	7.4 ± 2	1.3 ± 0.6	6.4 ± 4.4
Channel net + bongo net tow	2.4 ± 0.7	0.8 ± 0.3	7.0 ± 2

[1] n = 22 larvae.
[2] n = 18 larvae.
[3] n = 5 larvae.

EFFECTS OF HANDLING TECHNIQUE ON GUT CONTENT

In the laboratory, handling stress did not reduce the food quantities present in larval spot and pinfish, but did reduce the amount of food remaining in larval menhaden (Table 4). Two groups

TABLE 3.—Comparison of food quantities, mean number of copepods per fish ± one SE, present in larval spot (22-33 mm, $\bar{x}$ = 27 mm) collected by haul seine using rough and gentle handling techniques. Ten fish were collected per sample.

Date	Gentle	Rough
April 2	84.5 ± 7.4	78.6 ± 5.3
April 3	69.7 ± 5.9	66.9 ± 5.5

TABLE 4.—The effects of handling on the retention of *Artemia* nauplii in digestive tracts of larval Atlantic menhaden, pinfish, and spot. Rough handling is approximately equivalent to field capture by dip net and haul seine.

Species (Range mm)	Experiment 1		Experiment 2	
	Gentle	Rough	Gentle	Rough
	Mean number ± one SE			
Menhaden[1] (28-32)	71 ± 15	29 ± 10	145 ± 10	76 ± 11
Pinfish[2] (16-20)	37 ± 4	34 ± 5	35 ± 9	43 ± 6
Spot[2] (19-23)	51 ± 5	47 ± 5	89 ± 7	92 ± 10

[1] n = 18 larvae per sample.
[2] n = 36 larvae per sample.

of unfed larvae of each species were offered identical concentrations of *Artemia* nauplii. One group was handled roughly to represent the physical stress associated with field capture, while the other group was handled gently. The roughly handled fish were chased around the tank with a dip net for 10 to 30 s, captured with the net, allowed to suffocate in air, and then dissected. After feeding, the other fish were anesthetized by carefully adding an aqueous solution of MS-222 to the tank and then were dissected immediately to determine the numbers of nauplii in their digestive tracts. The roughly handled menhaden had only 40 to 52% of the *Artemia* numbers present in the guts of the gently handled menhaden (Table 4). The loss of food in menhaden larvae probably was due to the stress-related defecation or regurgitation and thus, may explain the consistently low quantities of food observed in larval menhaden captured in the estuary. Roughly handled pinfish and spot larvae showed no significant decrease in gut contents (Table 4). The curved digestive tract of larval spot and pinfish may prevent rapid passage of food, while the straight tubelike gut of menhaden may permit easy loss of food. This gut shape difference may account for the differences we observed.

A separate experiment was conducted to determine if the technique used to kill menhaden larvae in the handling experiments (exposure to air and suffocation versus anesthesia with MS-222) influenced the amount of food remaining in the gut. No difference was found. Fish killed by suffocation had a mean of 19 *Artemia* nauplii/fish (SE = 4.7), while fish anesthetized with MS-222 had a mean of 20 *Artemia* nauplii/fish (SE = 4.2).

EVACUATION RATES

Estimated regression coefficients for the equations describing the evacuation of copepods and *Artemia* nauplii are provided in Tables 5 and 6. Certain factors may alter the reliability of our estimates of evacuation rate under natural estuarine conditions. Bias may result from the temperature difference between estuarine waters from which fish were captured (14°-15°C) and the aquaria temperature during evacuation experiments (16°-17°C). The effect of a 2° temperature change on evacuation rate of larvae is unknown, although a similar change significantly increases the evacuation rates in some juvenile marine fish (Peters and Kjelson in press). Although our regression model could probably be improved, the r^2 values (Tables 5, 6) indicate the model is reasonable. Initial analysis included data collected until all the fish were empty. This resulted in nonlinearity near the end of evacuation due to bias near the end of evacuation period where more weight was given to the slower evacuating fish. Thus, by including in the regression analysis data from only those samples in which at least half of the larvae contained some food, this bias was decreased and the linear regression model appeared to represent larvae evacuation adequately.

TABLE 5.—Linear regressions describing evacuation of copepods in Atlantic menhaden, pinfish, and spot larvae. $Y = A + Bt$ where $Y = \log_{10}(1 + \text{mean number of copepods per larva})$ and t = hours since feeding. n = the number of data points.

Species	Mean TL (Range mm)	A	B	n	r^2	Temperature (°C)
Menhaden	29 (27-31)	1.14	−0.17	3	0.98	16
Pinfish	17 (15-20)	0.94	−0.10	3	0.86	16
Pinfish	16 (13-19)	0.68	−0.08	4	0.98	17
Spot	20 (17-23)	0.91	−0.10	5	0.98	17

INFLUENCE OF HANDLING AND CAPTURE ON EVACUATION

Evacuation experiments using *Artemia* nauplii were performed to determine if handling and capture influenced the rate of evacuation. Each

TABLE 6.—Linear regressions describing evacuation of *Artemia* nauplii in Atlantic menhaden, pinfish, and spot larvae under varied handling conditions. $Y = A + Bt$ where $Y = \log_{10}$ (1 + mean number of *Artemia* per larva) and t = hours since feeding. n = the number of data points.

Species	Mean TL (Range mm)	A	B	n	r^2	Handling condition	Temperature (°C)
Menhaden	29 (27-32)	2.36	−0.28	5	0.96	Gentle	15
Menhaden	29 (27-32)	2.04	−0.34	3	0.86	Rough	15
Pinfish	16 (14-18)	1.64	−0.26	4	0.97	Gentle	16
Pinfish	16 (14-17)	1.73	−0.28	3	0.92	Rough	16
Spot	20 (18-23)	2.12	−0.19	5	0.94	Gentle	16
Spot	20 (18-23)	2.11	−0.18	5	0.95	Rough	16

of the three larval fish species were fed concentrated amounts of *Artemia* (> 0.3 nauplius/cm^3) and allowed to feed until their digestive tracts were full. Each species then was transferred to food-free containers and separated into two groups, one handled roughly and another handled gently. Fish were sampled immediately and every 2 h thereafter. The rough treatment was similar to that used to study the influence of handling on gut content. The gently handled fish were sampled by dipping them carefully out of the tank with a beaker and anesthetizing them prior to dissection. The similarities of the regression coefficients (Table 6) for fish of the same species under the two treatments indicate that evacuation rates were not affected by rough treatment. The higher B value for roughly handled menhaden was not significantly different. Thus, our use of laboratory evacuation data to represent the normal evacuation in nature appears reasonable.

The regression coefficients for *Artemia* nauplii evacuation were larger (B values ranging from −0.18 to −0.34) than those for copepod evacuation (B values ranging from −0.08 to −0.17) for all three species (Tables 5, 6). This was expected since the *Artemia* nauplii were estimated to be only one-half the volume of copepods ingested by the larvae.

Food quality may also affect evacuation rate. Rosenthal and Hempel (1970) working with herring larvae found that *Artemia* nauplii were not digested as completely as copepods. We also observed that copepods become transparent in the posterior gut, whereas *Artemia* nauplii remained opaque.

The variation in the numbers of prey per larva between individual menhaden and pinfish larvae increased with each successive sampling period (0, 2, 4, 6, and 8 h after feeding stopped), but fluctuated in spot. The increasing variation in menhaden and pinfish may be explained by differences in individual evacuation rates. Food densities and gut capacities were relatively constant for the individual larva and thus, the initial numbers of prey per larva were similar. Varied individual evacuation rates would influence the amounts present in the tracts of the fish sampled at later times and therefore increase the variation. Individual fish may have significantly different evacuation rate constants as has been shown for juvenile pinfish (Peters and Hoss 1974).

DAILY RATIONS

The estimated daily rations for the three larval fish species varied between 3.5 and 9.0% of the mean wet weight of the fish or from 38 to 99 copepods/fish·day. The daily ration estimate for menhaden larvae (Table 7) was corrected by a factor of 2.5 to account for the fact that menhaden larvae lose approximately 60-68% of their gut contents during capture and subsequent handlings (Tables 2, 4). Since pinfish and spot larvae did not lose food from their gut when put under the stress, no correction factor was used.

Two estimates of daily ration, based upon both the 1972 and 1973 haul seine-dip net collections (Figure 1), are provided for spot larvae (Table 7). The two spot rations (4.3% and 9.0% of the body weight) differ considerably, probably due to differences in food availability.

Measurements of larval metabolic expenditures based on O_2 consumption (D. E. Hoss and W. F. Hettler, Jr., Atlantic Estuarine Fisheries Center,

TABLE 7.—Daily rations calculated from feeding studies and O_2 consumption measurements at 15°-17°C for larval Atlantic menhaden, pinfish, and spot in the Newport River estuary, N.C.

Species (range mm)	Mean larvae wet weight (mg)	Number copepods/ fish·day	Percent of body weight	Calories/ fish·day	Calories/fish·day estimated from O_2 consumption[1, 2]
1972:					
Menhaden (27-32)	43	53	4.9	1.18	3.0
Pinfish (16-20)	32	38	3.5	0.63	1.2
Spot (17-23)	33	47	4.3	0.78	1.2
1973:					
Spot (17-23)	33	99	9.0	1.65	1.2

[1]From Hettler and Hoss, unpubl. data.
[2]3.38 cal/mg O_2.

National Marine Fisheries Service, NOAA, pers. commun.) are higher than three of our four larval ration estimates (Table 7). Our menhaden ration of 1.18 calories/fish·day was 40% of the 3.0 calculated from Hoss and Hettler's measurements of respiration rate, indicating that for this species our estimate is probably low. Our pinfish ration was also lower, being 52% of that calculated from the O_2 consumption method. Our menhaden estimate is highly dependent on a very tentative factor used to adjust for handling effects. More accurate measurement of this conversion factor would probably provide better correlation with metabolic costs. Our 1972 spot ration was 66% of maintenance needs and may be indicative (as with pinfish and menhaden) of natural food shortages or environmental conditions not optimal for feeding on the dates of collection in 1972. The 1973 spot ration was nearly twice that estimated from O_2 consumption measurements and provides sufficient energy for general metabolism and growth.

We must consider our larval ration estimates as tentative in light of the high variability in the ration estimates for spot. This variation is due to differences in natural gut content, possibly as a result of differences in food availability on the sampling dates. Extensive sampling under the varied environmental conditions and zooplankton abundances and repeated evacuation rate measurements will provide us with more accurate estimates of their daily ration.

ACKNOWLEDGMENTS

We wish to express our sincere appreciation to Ronald L. Garner and Jerry D. Watson for their technical assistance during the entire study.

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